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AN ECOLOGIC VIEW OF THE SPECIES CONCEPTION

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I. PAST AND PRESENT PRACTISE IN SPECIES-MAKING

THE species may be either a means or an end; properly it is both. In descriptive botany, these two uses of the species have often been confused. The describing of new species has come to be recognized as an end in itself, while it should be nothing more than a necessary preliminary to further and more important botanical study. The interest of the ecologist in the proper recognition and naming of species is necessarily greater than that of nearly all other botanists. To him species are an indispensable means in the study of vegetation. On the other hand, the search for the definite results of adaptation and evolution, which is his final work, leads him inevitably to the species as an end. It is this double significance of the species for the ecologist that makes him peculiarly concerned about its treatment. So long as he uses the species only as a means, he is not greatly confused, except as a consequence of the fact that species are habitually made in the herbarium upon a small number of specimens, while he meets them as hundreds and thousands of variable individuals. His serious troubles begin with experimental work in adaptation and evolution. It quickly becomes evident that species so-called are widely different in rank, origin and relationship. Some are clearly species in the usual sense, while others are merely variations and forms of these. The ecologist thus comes to look with doubt upon all species. He accepts them reluctantly and provisionally until they meet successfully the test of experiment.

Even a casual survey of the practises in species-making during a century or more shows little or no uniformity of criteria or results. A comparison of methods in the different plant groups is even more striking. This lack of uniformity is found not only in the work of botanists in general, but even in the work of the same botanist. The consequences in the form of unequal and invalid species have been almost innumerable. This is particularly true of the fungi. To one familiar with them, it seems certain that the number of valid species is considerably less than half the number published. Attempts to guide the descriptive botanists and to make species more definite and uniform have not been wanting. A few of these have been noted, in order to show how little effect they had, even upon their own authors, and how utterly impossible of application they are without the test of experiment.

The criteria proposed by Ray were permanence of form and appearance, and non-fertility with other species. This appears to be little more than an attempt to justify the practise prevalent under the dogma of special creation. Mere observation could give little support to either criterion, and the thought of experimental support was scarcely dreamed of. As a pioneer in evolution, Lamarck gave a definition of the species, which would be expected to warrant more than passing interest. He defined a species as a "collection of similar individuals which are perpetuated in the same conditions as long as their environment is not changed sufficiently to bring about variation in their habits, their character or their form." It is clear that the whole value of this definition depends upon the significance given to the word variation. Lamarck, in his strong feeling for adaptation, hit upon the two essential facts, environment and variation, but his application of these criteria was purely academic.

It is a significant fact that Darwin should have written the "Origin of Species" without pointing out just what he meant by a species. His task was to prove origin by descent as opposed to origin by special creation. For this purpose, it was unnecessary as well as impossible to define a species or to discover the method by which it originates. Darwin regularly used the terms species, subspecies and variety, but he did not draw a definite and constant line between them. De Vries has taken the first definite step in advance by the use of experiment to determine a species. It remains to be seen whether his concept of elementary species will clarify or confuse. It can not be accepted even provisionally until much more experimental work has been done.

In the last decade or two, conservative American botanists have often expressed the view that proper specific characters can be drawn only from the flower and fruit, or from the reproductive parts, whatever they may be. Since this has sometimes been said to have been Dr. Gray's view also, it seemed that it would be both profitable and interesting to compare the criteria of conservative and radical describers of species in the same family and genus. Time was lacking for a thorough and complete comparison, but in the few families selected the results seem representative. It was quickly seen that many current species accepted by all were not based upon reproductive characters, and that some of the most doubtful of recent ones were. It further appeared that, while habit, leaf, stem, etc., played slightly more important parts in later work, there was little essential difference in the kind of criteria used. The striking difference lay in the fact that the new species segregated are based upon much smaller variations of the parts concerned, as a rule, and are consequently much more difficult to distinguish when represented by many individuals.

The ecologist finds it a necessity to be able to distinguish and to refer to any difference represented by a number of individuals. A form or a variation is just as important to him as a species, and often presents a better point of attack. He must consequently be partly in sympathy with the present tendency of descriptive botany to search out and describe all groups that are different, regardless of the degree of difference. He must, however, know the relationship of these groups, *i. e.*, whether they are coordinate species, forms or what not. To publish them all as binomials regardless of their rank completely hides their relationship to species already in existence. It is easy to understand that this has resulted partly from the fact that a trinomial is longer and hence less convenient than a binomial. Convenience is much less essential than accuracy and clearness, and must eventually yield to permit the regular use of the trinomial to designate the various differentiations of a species. The treatment of all groups below the genus as essentially coordinate is due even more to the fact that questions of ancestry and of origin enter all too rarely into the making of new species. These are questions that can be settled only by the most extensive and intensive field work, followed by thorough experiment. For such work there has as yet been almost no time or sympathy, as is shown by the all but hopeless mélange of so-called new species.

II. Bases for Distinguishing Species

The universal basis for distinguishing species has been the degree of morphologic difference. Physiologic and ecologic differences have but rarely been taken into account, except in such groups as the bacteria. The morphologic treatment is based upon the fundamental fact that stable structures are ancestral, and plastic ones derived. This has led to the basic principle that reproductive characters are of greater worth than vegetative ones. With this the ecologist is in full accord theoretically, but he would wish to have experimental evidence before accepting it as universally true. In fact some of the little evidence at present available indicates that this rule must permit some exceptions. It must constantly be borne in mind, especially by those who believe that evolution is always a question of the germ-plasm, that vegetative features alone are present in the blue-green algæ and many of the fungi. It is evident that the method of morphologic differences greatly facilitates the provisional cataloguing of a flora, but it suffers from a universal and serious fault. This is the use of a few herbarium specimens in lieu of a large number of field individuals. Practically every collector selects a few individuals that appear typical, while for the purpose of scientific species-making he should collect as complete a series as possible of divergent individuals. Even if this were done, the ecologist must continue to regard the method as a mere preliminary, which serves to arrange the material and hence to facilitate the real study of species.

Closely connected with morphologic difference is the question of the absence of intermediate forms. This appears to have played a more important part in zoology than in botany. In the latter case, at least, it seems often to have been taken for granted as a necessary consequence of structural differences. At best, it has regularly been a question of intermediate forms in the herbaria and not in the field.

Constancy as a criterion of species is also but another phase of morphologic difference. As such it seems to have been used chiefly to designate uniformity of difference throughout the individuals concerned. The constancy of a structure from one generation to another, or from one habitat to another has been given little attention in species-making. Yet it is precisely these which are of fundamental importance. This fact, however, makes it at once evident that constancy is something that can only be determined by combining the most extensive field observations year after year with experiments in various habitats. This makes it clear that our present knowledge of constancy is almost purely theoretical, and that it is profitless to discuss it in our present ignorance of it.

To the ecologist, then, the usual bases for distinguishing species, viz., degree of morphologic difference, absence of intermediate forms, and constancy, are entirely inadequate. He sees three critical facts in the development of a new species or any new form: (1) ancestry, (2) habitat or method of origin, (3) structural changes, very rarely functional ones. None of these can be studied adequately anywhere but on the ground. The first two are purely experimental questions. While the most thorough field study is a necessary preparation for them, they can never be decided except by experimental methods in the field. Apart from the study of the origin and structure of vegetation, the fundamental task of the ecologist is the experimental investigation of the origin of new forms, the so-called species.

III. ECOLOGIC PROCEDURE

The questions of what a species is, what are species and what are not, and of the origin of species and of forms must then be decided by experiment. The method of attack is easily determined, but the procedure is superlatively slow and laborious, and the demand upon time and patience unlimited. In spite of his inclination, the ecologist finds it necessary to accept as a working basis the species at present distinguished. His first task is to discover those that seem to give the best promise of results under experiment. The procedure consists of two essential processes: (1) field observations throughout the habitat of the species concerned and (2) experiment. The latter is the crux of the whole question. It consists of three steps: (1) the exact measurement by instruments of the original habitat and the new one, (2) the experiment itself and (3) the measurement of results, *i. e.*, the determination of the degree of morphologic and histologic difference. The detailed procedure in each of these has been given in "Research Methods in Ecology"[1] and it is unnecessary to repeat it here. It is sufficient to indicate that experiment should proceed whenever possible along three parallel lines, which have been designated as (1) natural experiments, where advantage is taken of natural movement into new habitats, (2) habitat cultures, where reciprocal plantings are made in original and new habitats, and (3) control cultures, where the experiments are carried on in plant-houses, where they can be controlled and directed at will. In addition to this, definite experiments for the determination and production of constancy are of fundamental value. In regard to the evaluation of the new form when once produced, it will suffice here to state that this should be concerned both with the individual and with the group of individuals. The proper determination of the latter is the task of biometry, when it has attained the necessary development.

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[1] Research Methods in Ecology, 25, 145.

For the preservation of the results obtained by the ecologic methods briefly sketched above, an *evolution herbarium* is proposed. It is felt that the usual taxonomic herbarium will have its usefulness restricted more and more to the preservation of types, and to the purposes of instruction. The evolution herbarium will be the record of field observations and experimental results. A species or a form will be represented in it by all the variations that can be discovered, and each variation by a large number of individuals. The new forms produced by nature, and by experiment in nature or under control, will likewise be adequately represented. This representation will take the form not only of the usual dried specimen, but of photographs, drawings, slides, preserved material, etc. With all this, however, the evolution herbarium is still to be regarded as a record merely. It is not to replace the taxonomic herbarium as a mass of working material to be shuffled about and made into species. It is a repository of species and forms when they have finally been determined by experiment.

IV. NOMENCLATURE AND TREATMENT OF NEW FORMS

Enough has been said to indicate clearly the ecologist's view of species, both valid and otherwise. He is vitally interested in the species' ancestry, its method of origin and the factor concerned, as well as in the result, which is the species or form itself. Until his experimental study of these points makes it possible to distinguish species from minor groups, or shows that the species concept is a mistaken one, it is useless to debate whether the resulting form is a species or not. In fact, the status of the result must await the determination of ancestry and origin in every case, and we may well call all the results forms until this has been done for each.

The question of ancestry resolves itself at the outset into one of old forms or of forms newly produced. The production of a new form from an old or existing one by properly checked experiment at once gives the ancestry of the former. Here, where the whole experiment is under our control from beginning to end, we may concentrate our attention upon the method of origin and the factor concerned. The discovery of the ancestor of an existing form or species is often a much more difficult matter. Until the ancestry is determined, it is useless to try to ascertain the method of origin, and the factor. When the form bears the distinct stamp of sun or shade, of a wet or dry habitat, or of hybridation, etc., our search is narrowed at once to deciding what species gives the most promise of being the parent form. When there is no distinct stamp, we must first look for the most promising species, and then try the various methods and factors experimentally until the form sought is produced. How often the ancestry and origin of accepted species can be worked out in this way remains to be seen. Results already obtained show that this method works perfectly in the few cases tried, and that it may be expected to prove successful in many cases. When a complete series of trials of suspected parents does not give the form sought, it seems fair to assume that these and the species sought are more or less coordinate. In this process, it is probable also that light will be thrown on the question of their derivation from a common stock or from two or more stocks.

The four methods by which new forms originate have been discussed before this society in a paper read last year. These have also been given in some detail in print[2] and are so generally well known to botanists that detailed consideration of them is unnecessary here. These four methods are adaptation, mutation, variation and hybridation. Variation alone has not yet been certainly established by experiment as a method by which new forms originate, but the evidence of it is so strong that it amounts to presumptive proof. It seems certain that for plants at least it is not the principal method, as Darwin thought, and that it is probably much less important than adaptation, and probably also less important than mutation. It is, however, a much more obscure process, and it is impossible to tell in the absence of any critical experiments just what it is, or what its importance may be. Darwin has said: "I have spoken of variations sometimes as if they were due to chance. This is a wholly incorrect expression. It merely serves to acknowledge plainly our ignorance of the cause of each particular variation." The exact measurement of habitats has made it clear that minute variation in the factors of the habitat is a very important if not the ruling cause in the production of minute variations in structure. In the case of the minute initial variations shown by the individuals of a group, it is impossible to tell at present how much is due to heredity and how much to causal variation of the habitat. It seems probable that the former may control in some forms, and the latter in others. Furthermore, while hybridation stands apart sharply from the others as a process in which existing characters are mixed in some degree, it is becoming more and more probable that adaptation, variation and mutation are only different phases, perhaps merely differences in degree, of the fundamental struggle between heredity and environment.

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[2] Research Methods in Ecology, 147; Plant Physiology and Ecology, 185.

Forms arising by adaptation have been called *ecads,* those from variation, *variants,* and those from mutation, *mutants.* With the familiar term *hybrid* for the product of hybridation, we are able to designate in a general way the forms originating by the four methods. The ecologist, and sooner or later the whole botanical world, must have some definite way of naming each particular form. It is possible to take no further thought about the matter, and allow this nomenclature to grow in the same random, unscientific fashion that nomenclature has always grown. It seems highly desirable, however, to consider the requirements of the case, and make suggestions as to the best method of meeting them. The first essentials of a name are that it should be as short and as significant as possible. For our present purpose, the name of each form should indicate the ancestry and the method of origin, and, when it is known, the causal factor. Many ways of securing this result have been considered for each method of origin. This may be illustrated by the following list, showing several possible ways of naming the shade ecad of *Galium boreale.*

1. *Galium dubiosum* n. sp.
2. *Galium boreale dubiosum.*
3. *Galium boreale.*[2]
4. *Galium borealades.*
5. *Galium boreale scias.*

The first method, which is that of descriptive botany at present, indicates nothing of ancestry, origin or factor. The second gives merely the ancestry, as does the third. The fourth gives both ancestry and method of origin, the patronymic suffix *-ades* referring to ecad. The use of a suffix has much to commend it, particularly the fact that it makes it possible to designate the forms of a species by means of a binomial. Its use, however, has practically been made impossible by the senseless names that have too often been given species. The fifth method, though requiring the use of the trinomial, is the best. It has all the brevity possible, and yet indicates ancestor, method of origin and factor concerned. It is interesting to note that this problem was worked out in 1902 in essentially the same fashion.[3] The shade form of *Galium boreale* was then called *Galium boreale hylocolum.* The present method has the advantage of brevity, and of referring directly to the causal factor concerned in producing the ecad rather than to the habitat as a whole. It is a relatively simple matter to recognize and produce sun and shade ecads, wet and dry ecads, but ecologic analysis can hardly go further at present. Consequently, the use of *scias, helias, xeras* and *hydras,* denoting respectively shade form, sun form, dry form and wet form, will not only enable us to designate all new ecads briefly and conveniently, but it will also reveal the ancestor, method of origin and causal factor at a glance.

After much puzzling, it seems that it will prove difficult, if not impossible to improve upon the conventional method of designating hybrids, viz., *Galium boreale* × *trifidum.* Until more is known of variants, it is proposed to designate them by a brief and applicable trinomial term, *e. g., Galium boreale exiguum.* While this is the usual trinomial, it would at once reveal the method of origin, as well as the ancestor, by virtue of the fact that the other three methods of origin have their proper trinomial form. In our present knowledge of mutants, it seems impossible to take the cause into account. The suggestion is accordingly made that the mutant be named with reference to its most striking characteristic, the trinomial term to bear the prefix *per,* very, referring to the saltatory nature of mutation, and thus denoting the method of origin. The value of these suggestions may be indicated by comparing the trinomials thus formed with the corresponding binomials.

[3] Herbaria Formationum Coloradensium.

Cerastium oreophilum = *Cerastium strictum scias:* ecad.
Verbena intermedia = *Verbena stricta* × *hastata:* hybrid.
Aquilegia jamesii = *Aquilegia cœrulea peralba:* mutant.
Machæranthera aspera = *Machæranthera viscosa aspera:* variant.

In concluding, the ecologist will confess frankly that he does not know what a species is. On the other hand, he is certain that he knows some of the things it is not, and that the species of the descriptive botanist comprise several widely different things. Just what these are and what their relation to species, if there are such, is a matter to be decided by experiment alone. The question of what a species is can not even be answered provisionally until a sufficiently large number of experiments have been made to indicate the regular procedure in the origin of plant forms and to reveal the principles that control it.